GENETIC STUDIES IN POULTRY.

IX. THE BLUE EGG.

By R. C. PUNNETT, F.R.S.

(With Plates XXII and XXIII.)

Introduction.

The existence of hens laying blue eggs was first brought to the general notice of the poultry world by Prof. Salvador Castello Carreras during the meeting of the First World's Poultry Congress at The Hague in 1921. He stated that he had met with them when travelling in Chile in 1914, and in the brief account[1] which he gave proposed for them the name *Gallus inauris*, partly in recognition of the "muff" which is so frequently found among them, and partly because he was inclined to believe "that these hens descend from the hens which the Missionaries of the sixth and seventh centuries[2] pretend to have seen in the south of America at the time of the conquest by the Spaniards and who assert in their writings that *they were quite different from the Castilian hen.*"

But in his interesting article[3] on "The Araucano, the Blue-egged Fowl of Chile," C. A. Finsterbusch considers that "it has been fairly proved that there were no fowls there before the advent of the white man in S. America." He brings forward evidence suggesting that the Spanish poultry originally imported were subsequently reinforced by Balinese birds through the efforts of Dutch pirates, and points out that birds of typical Oriental types are common among the mongrel population of Chile. Further, he makes it clear that the fowl population of Chile is just as mongrelised in respect of egg colour as of structural features and plumage. Commenting on the "blue" egg, he states that "these strange-coloured shells are, however, by no means of uniform tint. There are bluish, blue-grey, purplish, greenish, greyish green, and, finally, greenish eggs speckled with brown, which indicates clearly some precedent colour influence, either abnormal or incidental." Finsterbusch suggests that the greenish and bluish shell colour is due to loss of the red pigment brought in by the imported stock from Bali. As will appear later, this explanation does not accord with the genetical data.

[1] *Trans. First World's Poultry Congress at The Hague-Scheveningen*, 1921, pp. 59–62.

[2] Presumably a misprint for "sixteenth and seventeenth centuries."

[3] *The Feathered World*, August 28, 1931.

Experimental data.

In the summer of 1930 I acquired three Chilean hens through the kindness of Mr Claud Elliot who had brought them over direct from Chile. They were evident mongrels at sight, differing widely in plumage colour and structural features. One died soon after arrival, but the two survivors both laid blue eggs. Though it was late in the season I managed to rear a few chicks (5 ♂♂ and 2 ♀♀) from one of the hens, a nondescript yellow, mated with a Gold-Pencilled Hamburgh cock. These F_1 birds form the basis of the experiments set out in Table I.

Of the two F_1 pullets one (368) laid a blue and the other (385) a white

TABLE I.

Year	Pen No.	♂	♀♀	Nature of mating	Nature of Daughters
1930	10	Gold Hamb.	Chilean	(wh.) × het. blue	1 blue (=♀ 368) 1 non-blue (=♀ 383)
1931	8	Welsummer	Chilean	(brown) × het. blue	2 olive (♀ 246, ♀ 311) } blue 1 green (♀ 185) } 2 brown } non-blue 2 tinted }
—	16	F_1 383	F_1 385	(het. blue) × white	5 blue 5 non-blue
—	17	F_1 370	F_1 368	(het. blue) × het. blue	2 blue (♀ 399)
—	—	—	2 Lt. Sussex	(het. blue) × tinted	6 blue 8 non-blue
1932	16	F_1 383	2 F_1 ex Lt. S.	(het. blue) × het. blue	20 blue 10 non-blue
—	18	183	399	(wh.) × blue	8 blue
—	21	Welsummer	246	(brown) × olive	1 olive
—	—	—	311	(brown) × olive	1 olive 1 deep brown
—	—	—	185	(brown) × green	2 olive 2 brown

egg. Since the Gold-Pencilled Hamburgh is a white-egg breed the result at once suggested that blue might be a simple dominant, and this has been confirmed by subsequent work. In 1931 each of these two F_1 pullets was mated with a brother (cf. Table I). Of the daughters of 385, which laid a white egg, five laid blue and five laid non-blue eggs. This is in accordance with expectation on the assumption that F_1 ♂ 383 was heterozygous for the blue factor, an assumption confirmed in the following year. ♀ 368 with F_1 ♂ 370 produced only two daughters, both of which laid blue eggs. But ♂ 370 was also mated with two Light Sussex pullets, both layers of pale brown eggs. From this mating 14 daughters were tested in 1932. Six laid blue and eight laid non-blue eggs. ♂ 370, like ♂ 383, is therefore to be regarded as heterozygous for the blue factor. This was confirmed by the fact that one of his daughters (♀ 399) from his sister (♀ 368) proved to be homozygous for blue. For, mated with a cock of a white-egg strain (♂ 183) in 1932, she produced eight daughters, all of which laid blue eggs in the following year.

Two of the "blue" daughters from the mating between ♂ 370 and the Light Sussex pullets were mated in 1932 with ♂ 383. Since the evidence of the previous year showed him to be heterozygous for blue such a mating should result in "blue" and "non-blue" daughters in the ratio 3 : 1. Of the 30 daughters tested in 1933, 20 were "blue" and 10 were "non-blue," a proportion not far removed from expectation. All of the evidence is in accordance with the view that blue is dominant to non-blue, and is dependent upon the operation of a single factor.

In the experiments so far dealt with the non-blue egg was either white or lightly tinted. The blues differed a little in shade, some having a slightly more greenish tinge than others. Presumably the clearest blues were those in which the blue was on a white ground, the greenish tinging in others being due to a tinted ground. Experiments were also undertaken with a view to finding out how the blue behaved when associated with the deeper brown colour characteristic of the eggs of certain breeds of poultry. For this purpose the other original Chilean hen was mated in 1931, with a Welsummer cock—a breed in which the colour of the eggs is deep brown. Of the seven daughters tested two laid brown (Pl. XXII, fig. 1) and two laid rather markedly tinted eggs (Pl. XXII, fig. 3), all of which may be reckoned as belonging to the non-blue class. But one laid a definitely green egg (Pl. XXII, fig. 4) and two laid eggs of a deep olive colour (Pl. XXII, fig. 2) recalling that of a normal pheasant's egg. These last three birds must be supposed to carry the blue factor. The production of the paler types, viz. tinted and green, I regard as being due to the Chilean hen being heterozygous for a factor partially inhibiting the production of brown, for the existence of which I have given reasons elsewhere[1]. In the following year the three birds laying eggs of the blue class, viz. two olive and one green, were put back to their Welsummer father, but owing to his early demise in 1932 few offspring were raised. However, such as were produced were in accordance with expectation. The "olive" pullets (♀ 311 and ♀ 246) gave between them three daughters of which two laid olive and one laid deep brown eggs. The "green" pullet (♀ 185) gave two

[1] *Heredity in Poultry*, 1923, pp. 168–72.

"olive" and two "deep brown" daughters. Normally some tinted and green were also to be expected, but their absence cannot be regarded as significant where the numbers are so few.

These experiments show that although "blue" and "brown" may be combined to give "olive," they are nevertheless transmitted independently. And here may be considered the manner in which these pigments affect the shell. The blue shell is blue throughout. This is at once apparent when the shell membrane is stripped from the inner surface of the shell. Moreover, the green and the olive eggs also appear blue when viewed from the inside. This permeation with blue renders the shell much more opaque, a fact at once noticed when the eggs are "candled" in the early stages of incubation.

On the other hand the brown pigment is superficial, and presumably only laid down during the last stage in the passage of the egg along the oviduct. The various shades of brown are dependent upon several genetical factors as yet incompletely analysed. But in a general way the position is somewhat as follows[1]. The deep brown egg is due to the action of several factors of which one produces a considerably greater effect than the others. The deepest colour results when the bird is homozygous for the minor factors as well as for the major one. In the absence of the latter the egg is light brown, and in the absence of all the colour factors it is white. Shades varying from pale tinted to light brown result when the birds are of different constitutions for the minor factors and at the same time lack the major one. The matter is further complicated by the existence in some breeds of an inhibitor factor restricting the action of the pigment-producing factors. When this is present the colours of the brown series are greatly reduced throughout. Thus, what would normally be a deep brown egg becomes pale brown in the presence of the inhibitor, while the lighter tinted eggs become white or nearly so. The two original Chilean hens were probably heterozygous for this inhibitor, since, with the Welsummer cock, they gave approximately equal numbers of daughters laying brown or olive eggs on the one hand, and tinted or green on the other. The Light Sussex pullets used laid light brown eggs. That they were not potential dark brown layers which also carried the inhibitor was proved by mating them with the Welsummer cock. For all the pullets so produced laid dark brown eggs, though not quite of such a deep colour as those of the Welsummer itself. This accords with the fact that all of the 30 pullets bred from Light Sussex × F_1 ♂ 370, when crossed back with F_1 ♂ 383, laid only bluish or white or pale tinted eggs. For it is

[1] Cf. *Heredity in Poultry*, 1923, pp. 164–73.

likely that in this cross both parents carried the inhibitor factor. These results also show that the factor inhibiting the production of brown pigment has little or no influence on the blue.

DISCUSSION.

The results taken as a whole support the view that the blue and brown pigments are genetically independent, though what are the chemical relations between them is not yet clear. The brown colour depends upon protoporphyrin, a derivative of haemin, but the nature of the blue is yet uncertain. Dr Rudolf Lemberg[1] found the blue pigment of the egg shells of the black headed gull (*Larus ridibundus*) to be oocyan, a substance closely related to the bile pigments. At my request he kindly examined some of the blue hens' eggs, and communicated the result to me in a letter. Curiously enough he found that the blue pigment here was not oocyan, although small traces of oocyan were also present. Dr Lemberg's investigation has not proceeded sufficiently far to allow of certain identification, but he considers it probable that the blue pigment is the so-called "banded oocyan" of Sorby. Whether its production depends upon a specific enzyme, present only in the layers of blue eggs, is as yet undetermined, but the genetical evidence suggests that this is not unlikely.

A further point of interest attaching to these blue eggs lies in the parallel which they suggest between the hen and the pheasant. Breeders of the commoner pheasants (*P. colchicus*, *P. torquatus*, and *P. mongolicus*) are well aware that in respect of egg colour they can be highly polymorphic. To the kindness of my friend, Mr H. C. Eltringham, I owe a small collection of pheasants' eggs from which I have figured six examples on Pl. XXII. A comparison between this plate and Pl. XXIII serves to illustrate the close parallelism that exists in variety of egg colour between the pheasant and the hen, allowances being made for the differences in shell texture. In either case there exists a brown series in which the interior of the shell is white or whitish, for in either case the brown pigment is confined to the outer surface of the shell. Corresponding to this brown series there exists in either case an olive-green-blue series in which the substance of the shell is blue throughout. No genetical data exist for the pheasant, but I have little doubt that suitable experiments would show the relations between the various colours of egg in these species to be similar to those here demonstrated for the fowl.

As to how the blue factor entered into the composition of the domestic hen we can offer no plausible suggestion. None of the wild species of *Gallus*

[1] "Über Oocyan I." *Liebig's Ann.* **488**, 74, 1931.

lays an egg which can be supposed to contain it. Among the true pheasants (*Phasianus*), judging by the recorded colours of the eggs, it is to be found in some species though not in others[1]. It is well known that hybrids can be readily obtained between the pheasant and the domestic fowl, but hitherto such hybrids have proved to be sterile. It cannot, however, be said that the matter has been fully explored, and it is conceivable that at some time or other fertile offspring may have been produced. But in that case one would expect to find some evidence of this among the domestic fowls of the East Indies. In its absence we can only suppose that the blue egg arose as a dominant mutation among domestic fowls in South America, and probably among those imported from Asia by the Dutch.

Note added June 20, 1933. Since the above was printed I have received an interesting communication from Mr A. P. Thompson of *The Feathered World*. A correspondent of his, belonging to the firm J. E. van der Laat Sucr., St José, Costa Rica, states in a letter dated April 28, 1933, that "the original hens of Costa Rica lay an egg of an absolutely brilliant green colour. These hens are found in the mountains and are very difficult to obtain. The people call them 'Golondonas' or 'Gallinas de Monte.' I found last week a nest with two eggs, and I put them in one of my incubators and am awaiting now the result." It seems likely that the "brilliant green" egg may be blue on yellowish tinted ground, similar to that represented on Pl. XXII, fig. 4.

Summary.

The blue egg character, common among fowls in parts of Chile, behaves as a simple dominant to non-blue. Combined with the various shades of brown it gives a series of greens and olives. Polychromatism in fowls and pheasants' eggs follows apparently similar lines.

EXPLANATION OF PLATES XXII and XXIII.

Plate XXII.

Figures illustrating polychromatism in fowls' eggs. 1, brown; 2, olive; 3, pale brown; 4, green; 5, white; 6, blue.

Nos. 2, 4 and 6 are shades in the "blue" series corresponding with Nos. 1, 3 and 5 in the "non-blue" series. Many intermediate shades may occur in both series.

Plate XXIII.

Figures illustrating polychromatism in pheasants' eggs. The colours have been arranged to correspond with those on the preceding plate.

[1] See W. R. Ogilvie-Grant's *Handbook to the Game-birds*, vol. II, London, 1897.